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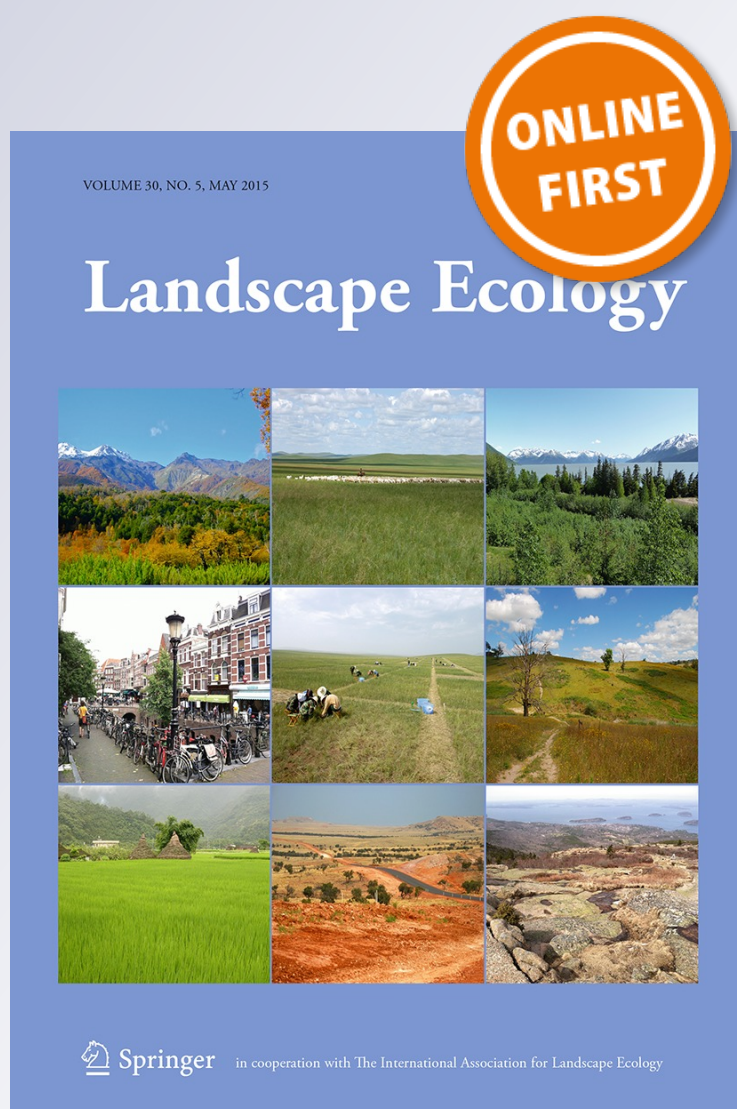
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## RESEARCH ARTICLE

# Climate-induced lake drying causes heterogeneous reductions in waterfowl species richness

Jennifer K. Roach · Brad Griffith

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## Abstract

**Context** Lake size has declined on breeding grounds for international populations of waterfowl.

**Objectives** Our objectives were to (1) model the relationship between waterfowl species richness and lake size; (2) use the model and trends in lake size to project historical, contemporary, and future richness at 2500+ lakes; (3) evaluate mechanisms for the species–area relationship (SAR); and (4) identify species most vulnerable to shrinking lakes.

**Methods** Monte Carlo simulations of the richness model were used to generate projections. Correlations between richness and both lake size and habitat diversity were compared to identify mechanisms for the SAR. Patterns of nestedness were used to identify vulnerable species.

**Results** Species richness was greatest at lakes that were larger, closer to rivers, had more wetlands along

their perimeters and were within 5 km of a large lake. Average richness per lake was projected to decline by 11 % from 1986 to 2050 but was heterogeneous across sub-regions and lakes. Richness in sub-regions with species-rich lakes was projected to remain stable, while richness in the sub-region with species-poor lakes was projected to decline. Lake size had a greater effect on richness than did habitat diversity, suggesting that large lakes have more species because they provide more habitat but not more habitat types. The vulnerability of species to shrinking lakes was related to species rarity rather than foraging guild.

**Conclusions** Our maps of projected changes in species richness and rank-ordered list of species most vulnerable to shrinking lakes can be used to identify targets for conservation or monitoring.

**Keywords** Alaska · Biodiversity · Climate warming · Lake change · Lake size · Species–area curve

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## Introduction

Landscape change in response to climate warming has been quantified both spatially and temporally for a range of ecosystems including shrub tundra (Sturm et al. 2001; Tape et al. 2012), forests (Hansen et al. 2010), glaciers (Arendt et al. 2002), and lakes (Smith et al. 2005; Roach et al. 2013). However, little has

been done to spatially and temporally link landscape change to quantifiable effects on wildlife populations, biodiversity, or ecosystem services. This linkage is the essential next step toward using landscape-scale research to inform land management and policy decisions. Here, we use a novel approach to quantify the effects of both historical and future landscape-scale changes in lake size on waterfowl biodiversity in an ~1 million ha National Wildlife Refuge (NWR) study area in Alaska, USA.

Climate warming has been associated with net declines in lake size across broad spatial extents throughout the circumpolar, including Canada (Carroll et al. 2011), Siberia (Smith et al. 2005), and Alaska (Riordan et al. 2006; Roach et al. 2013). NWRs in Alaska comprise 82 % of the area of the entire NWR system (Meretsky et al. 2006) and were originally established for the preservation of critical breeding habitat for waterfowl (Braun et al. 1978) that migrate annually to almost all continents. Therefore, it is of particular concern that six NWRs in Alaska have had declining trends in lake size since ~1985 (Klein et al. 2005; Roach et al. 2013). Shrinking lakes in Alaskan NWRs could have both local and far-reaching implications for waterfowl biodiversity and ecosystem services.

Climate-related mechanisms that have been proposed to explain declines in lake size vary depending on the location and scale of the investigation. These mechanisms include increased evapotranspiration (Smol and Douglas 2007; Anderson et al. 2013; Lewis et al. 2014), terrestrialization and floating mat encroachment on lake surfaces (Roach et al. 2011), and permafrost degradation leading to either increased substrate permeability and drainage to groundwater systems (Yoshikawa and Hinzman 2003; Smith et al. 2005; Karlsson et al. 2012; Jepsen et al. 2013; Roach et al. 2013) or melting of ice wedges that results in lateral breaching of lake shorelines (Jones et al. 2011; MacDonald et al. 2012; Necsoiu et al. 2013).

Independent of the mechanism involved, relationships between lake characteristics and waterfowl species richness can be used to quantify the effects of shrinking lakes on waterfowl. Positive species–area relationships (SARs) have been identified for waterfowl at lakes in Scandinavia (Elmberg et al. 1994), Switzerland (Suter 1994), and Spain (Paracuellos and Tellería 2004). If present in high-latitude ecosystems, these relationships might indicate vulnerability of

waterfowl to shrinking lakes and provide a means to project the effects of future declines in lake size on richness. In fact, by identifying the mechanisms underlying a positive SAR, we may be able to identify species that are most vulnerable to declines in lake size.

Four primary mechanisms have been proposed to explain SARs (Connor and McCoy 1979; Nilsson et al. 1988; Cam et al. 2002; Schoereder et al. 2004): three (passive sampling, area *per se*, and habitat heterogeneity) are based on ecological processes and one is a sampling artifact. The sampling artifact arises when more samples are collected from large areas than small areas in an attempt to more fully characterize the larger area. Collecting more samples from a species pool increases the probability of collecting more species (Hill et al. 1994). Thus, an SAR could result solely from differences in the number of samples and no ecological mechanism needs to be present.

Passive sampling is an ecologically based mechanism for SARs and is often confused with sampling artifact (Cam et al. 2002; Schoereder et al. 2004). In passive sampling, it is the size of the area of suitable habitat, not the number of samples taken from suitable habitat that is assumed to affect the number of species present. A larger area of suitable habitat contains a single larger effective sample from the species pool than does a small area (Connor and McCoy 1979) and the number of species present increases concurrently. Passive sampling is considered an ecologically based mechanism of SARs because the number of species present is a function of suitable habitat area, not sampling design.

A second ecologically based mechanism of SARs, “area *per se*,” postulates that the number of species in an area depends on the balance between immigration and extinction, which are directly related to population size and in turn to the size of an area of interest (MacArthur and Wilson 1967; Connor and McCoy 1979). These classic concepts of immigration and extinction do not directly apply to our system, because species observed at a lake are not permanent residents. However, a variant of area *per se* might exist whereby larger lakes simply provide more space and resources and thus support larger transient populations (Patterson 1976; Nudds and Ankney 1982; Heglund et al. 1994). Because this variant of area *per se* is difficult to distinguish from passive sampling we will henceforth refer to both the area *per se* and passive sampling hypotheses as passive sampling.



The “habitat diversity hypothesis” (Williams 1964) assumes a positive relationship between area and habitat heterogeneity (Nilsson et al. 1988). This ecologically based mechanism predicts that large areas will have more species because they tend to have greater habitat diversity (Hart and Horwitz 1991; Elmberg et al. 1993). Because nesting habitat preferences vary among waterfowl species and between foraging guilds (e.g., dabblers, divers; Kiminsky and Weller 1992), greater habitat diversity may promote waterfowl species richness. If this is the case, then a loss of habitat diversity may have a large effect on a particular waterfowl species or species guild if their preferred habitat is lost.

To differentiate between the passive sampling and habitat diversity hypotheses, we can examine the types of species that are most vulnerable to shrinking lakes. For example, the number of dabbling duck species has been shown to be dependent on habitat diversity (Elmberg et al. 1993). However, dabbling ducks may also have greater plasticity to habitat change than diving ducks (Nudds 1983). Alternatively, if passive sampling is more important to waterfowl species richness than habitat heterogeneity, the species most vulnerable to shrinking lakes may instead be those that are least abundant (Cutler 1994) regardless of their habitat preference (e.g., rare species on the edge of their range). By identifying the species most vulnerable to shrinking lakes, we can understand the relative roles of habitat heterogeneity and passive sampling in determining species richness.

Scientists can use patterns of nestedness in conjunction with future projections of lake size and number derived from species–area curves to identify waterfowl species that are vulnerable to climate-induced lake shrinking. Perfect nestedness occurs when communities form perfectly nested subsets with species in species-poor habitats constituting subsets of those present in species-rich habitats (Darlington Jr 1957; Ulrich et al. 2009). A perfectly nested matrix has been described as having a completely replicable extinction order where each species goes extinct in turn as it falls below a minimum sustainable population size (Atmar and Patterson 1993). Although perfect nestedness is rare, tests have been designed to evaluate whether groups of sampling sites approximate a nested subset structure (Atmar and Patterson 1993; Rodríguez-Gironés and Santamaría 2006). When an approximate nested subset structure is

present, and the size and, thus, species richness of individual sampling sites (e.g., lakes) change, the species most likely to be gained or lost to yield the new community are those that bring the system closer to perfect nestedness. For example, a species will be vulnerable to declines in lake size if it is present at a lake where the species is expected to be absent under a scenario of perfect nestedness. Thus, patterns of nestedness can be used to predict orderly patterns of species loss or gain and identify the species most vulnerable to change (Bolger et al. 1991; McDonald and Brown 1992; Kerr et al. 2000; Paracuellos and Tellería 2004).

In order to better understand how projected changes in lake size may affect the number, type, and identity of waterfowl species at lakes in Alaska, USA, we addressed the following objectives:

- (1) Model the relationship between species richness and lake size plus other broadly mapped landscape covariates.
- (2) Use the waterfowl species richness model in (1) in conjunction with trends in lake size (Roach et al. 2013) to spatially and temporally project historical and future changes in waterfowl species richness.
- (3) Evaluate the relative roles of habitat heterogeneity and passive sampling as drivers of species richness at lakes.
- (4) Use patterns of nestedness to identify species most vulnerable to decreasing lake size.

Because lake change is spatially heterogeneous (Riordan et al. 2006; Carroll et al. 2011; Roach et al. 2011, 2013), the ability to project changes in waterfowl species richness at a variety of spatial extents is necessary. Our work may enable land managers to identify lakes or regions where richness may be stable or increasing, despite the presence of declining trends at a broader spatial extent. Thus, these results may have implications for choosing sites for conservation or monitoring.

## Methods

### Study area

The Yukon Flats NWR (hereafter, “The Refuge”) is the third largest in the NWR system and has a diverse

mosaic of vegetation communities representative of the broader boreal forest ecosystem (<http://www.fws.gov/refuges/profiles/History.cfm?ID=75635>). Our study area (146°58' W, 66°19' N) included three sub-regions (West, Central, and East; Fig. 1) where previously estimated trends in lake size from 1986 to 2008 (−2.96 to +0.34 % change per year) encompassed the full range of trends that had been observed in study areas across Alaska (Roach et al. 2013). This choice of study area should increase the applicability of this work to a broader area. The boundaries of our study area and sub-regions (Fig. 1) were delineated to encompass lake-dense lands of particular value to waterfowl populations and other ongoing studies identified through consultations with Refuge staff.

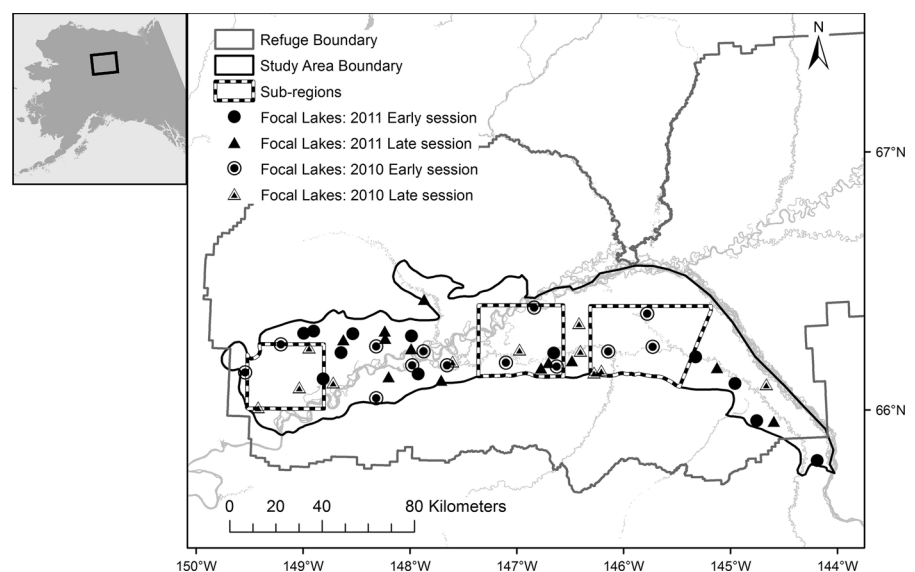
Data were collected at 48 focal lakes and 75 satellite lakes located near these focal lakes. Focal lakes were selected from the population of float plane landable (Cessna 185<sup>TM</sup>, de Havilland Beaver<sup>TM</sup>) lakes using a generalized random tessellation stratified sampling design. This design has the advantages of both random sampling (i.e., probability design enabling inferences to be drawn for an entire population or area) and systematic sampling (i.e., generates a spatially balanced sample where focal lakes are not clumped together; Stevens and Olsen 2004). Satellite lakes within or intersected by a 1 km radius around the focal lake centroids were assigned a random order and sampled in that order until all satellite lakes were sampled or until a maximum of 14 days elapsed.

Because focal lakes were selected from float plane landable lakes, our sample of lakes tended to be larger than the population average (sample: mean = 37 ha, standard deviation = 62 ha, population: mean = 8 ha, standard deviation = 26 ha). However, the inclusion of smaller-sized satellite lakes ensured that lakes of all sizes were well represented in our sample. A purely probability-based sample may not have captured the full range of lake sizes because large lakes were rare. The final set of lakes used to build the waterfowl richness model included 24 focal lakes and 31 satellite lakes sampled during 2010 and 24 focal lakes and 44 satellite lakes sampled during 2011.

### Waterfowl surveys

We used an expanded definition of the term “waterfowl” that included loons (Gaviiformes), grebes (Podicipediformes), and coots (*Fulica americana*) in addition to ducks, geese, and swans (Anseriformes). Each lake was surveyed during an early (6 June–1 July) or late (25 July–20 August) summer session in 2010 or 2011. At each lake, one point count survey and one supplemental survey were conducted each day for at least 2 days in 2010 and for at least 3 days in 2011. There were 10 observers. The same observer conducted all surveys for a focal lake and its satellite lakes. Sampling began at sunrise and stopped after 6 h or when the entire lake had been surveyed or weather conditions prevented survey completion.

**Fig. 1** Spatial distribution of 48 sampled focal lakes by year and session, Yukon Flats National Wildlife Refuge, Alaska, USA, 2010 and 2011



Point count surveys began along a random bearing from the lake center. The direction walked from the start point was random. Points were 200 m apart and were 100 m from the lake shore or at the edge of the shrub or forest perimeter if less than 100 m from the lake. Bird observations within a 100 m radius from each point were recorded for 10 min. Supplemental surveys began at the last point count. Observers walked in the opposite direction of the point count survey through the herbaceous habitat recording all waterfowl seen on the lake or on land and ending at the starting point count. Spotting scopes and binoculars were used to identify birds. To maintain consistency between years, we estimated relative waterfowl species richness as the total number of species observed during the first two point counts and supplemental surveys at each lake. Due to observer variability and limited time for sampling, we likely did not observe every waterfowl species ever present at each lake. Thus, we consider our estimates of waterfowl species richness to be relative, as opposed to absolute, which can be reliably compared between lakes and years due to our consistent sampling approach among lakes.

#### Waterfowl species richness model

We used a Poisson generalized linear mixed model to quantify the relationship between relative waterfowl species richness and lake size as well as several other lake characteristics for our sample of 123 lakes (SAS Institute, Inc. 2002–2010; Proc GLIMMIX Procedure) (Appendix 1). Random effects enabled us to account for observer variability and spatial autocorrelation (Appendix 1). We used standard diagnostic methods (Agresti 2007) to confirm that the assumptions of a Poisson regression model (e.g., no overdispersion) were adequately met.

We restricted our analysis to independent variables that had been broadly mapped for our entire study area so we could use the model to generate projections for all ~5500 un-sampled lakes in the study area. We considered the following covariates when building the model: (1) lake size, (2) sample session, (3) shoreline irregularity ( $\text{perimeter}/(2(\text{area} * \pi))^{1/2}$ ; Kalff 2002), (4) elevation, (5) distance to nearest river, (6) diversity of land cover types along the lake perimeter (Shannon 1948), (7) proportion of lake perimeter in emergent wetland, (8) proportion of lake perimeter in any wetland type, (9) isolation (i.e., distance to the nearest

lake), (10) number of lakes within 5 km, (11) density of lakes within 5 km, (12) mean lake size within 5 km, (13) size of the largest lake within 5 km, and (14) coefficient of variation in lake sizes within 5 km (Appendix 2). We chose a distance of 5 km for the surrounding lake matrix covariates because this distance encompassed the mean home range size for all observed waterfowl species including those with both small (8–27 ha) [e.g., northern shoveler (*Anas clypeata*) and gadwall (*Anas strepera*) Gates 1962] and large (210–998 ha) home ranges [e.g., northern pintail (*Anas acuta*); Derrickson 1978, mallard (*Anas platyrhynchos*) Gilmer et al. 1975; Dwyer et al. 1979; Kirby et al. 1985; Mauser et al. 1994 and canvasback (*Aythya valisineria*) Dzubin 1955]. We did not consider the interaction terms to increase simplicity in model interpretation, which may enhance management value, and because of computational limitations in the number of possible terms that we could consider in our mixed models in a reasonable time. Independent variables were transformed when necessary to enable model convergence and were centered and scaled for ease of model interpretation (Schielzeth 2010) (Appendix 1). Corrected Akaike's information criteria were compared to identify the best model that did not include collinear variables (Appendix 1). We tested correlations between richness and a number of other variables that were not considered in our model due to their inability to be broadly mapped but that might have a direct or indirect mechanistic link to richness (i.e., lake depth, surface-to-volume index, water temperature, and conductivity).

We calculated a species richness detectability index for 76 lakes that had both point count and supplemental surveys conducted for at least three consecutive days. The detectability index for each lake was the proportion of species observed in 3 days that were also observed in 2 days. To evaluate whether differences in detectability among lakes may have led to false identification of relationships between covariates and waterfowl species richness at sampled lakes, we regressed the detectability index against each covariate in the final model for the subsample of 76 lakes. A significant ( $\alpha = 0.05$ ) relationship between the detectability index and a covariate would indicate that relationships between that covariate and species richness may have been due not to differences in true species richness among lakes, but instead to differences in detectability among lakes.

## Retrospective waterfowl species richness projections

For all lakes ( $n = 2565$ ) within the three sub-regions, we used the waterfowl species richness model to generate retrospective projections of waterfowl species richness for 1986 and 2010. We used back-casted estimates of lake size derived from linear trends estimated by Roach et al. (2013) from a series of six Landsat images from 1986 to 2008. To generate retrospective waterfowl species richness projections, we used a two-phase Monte Carlo simulation (R Core Team 2013) that accounted for observer variability and the error from both the lake trend and the waterfowl species richness models. For the first phase, we randomly selected 100 estimates of lake size for each lake from normal distributions with a mean and standard deviation equal to the fitted value and its standard deviation, respectively, from the lake trend model where day of summer was set to 15 July and year was set to either 1986 or 2010.

For the second simulation phase, we entered these 100 simulated values of lake size for each lake into the waterfowl species richness model to generate 100 corresponding estimates of species richness along with their associated standard errors. Then, for each of these estimates of species richness, we took 100 random draws from a normal distribution with a mean equal to the species richness estimate from the species richness model and a standard deviation equal to the standard deviation of the estimate. This process yielded a total of 10,000 simulated values of waterfowl species richness for each lake and for each time period. Because these richness distributions were positively skewed, we used the median value of each distribution of 10,000 simulations to represent the species richness projection for each lake and the quartile coefficient of dispersion (Bonett 2006) to represent the relative error associated with each projection.

For each simulation of the waterfowl species richness model, we assigned a random observer from the list of 10 observers used to build the original model. To estimate the covariates in the waterfowl species richness model other than lake size (e.g., distance to nearest river) for all lakes in the three sub-regions, we applied methods for covariate estimation (Appendix 2) to polygons corresponding to the maximum extent of each lake derived from six images from 1986 to 2008 (Roach et al. 2013) and held these

constant through time. We used maximum extent polygons in order to capture the full range of seasonal variability in lake size from 1986 to 2008.

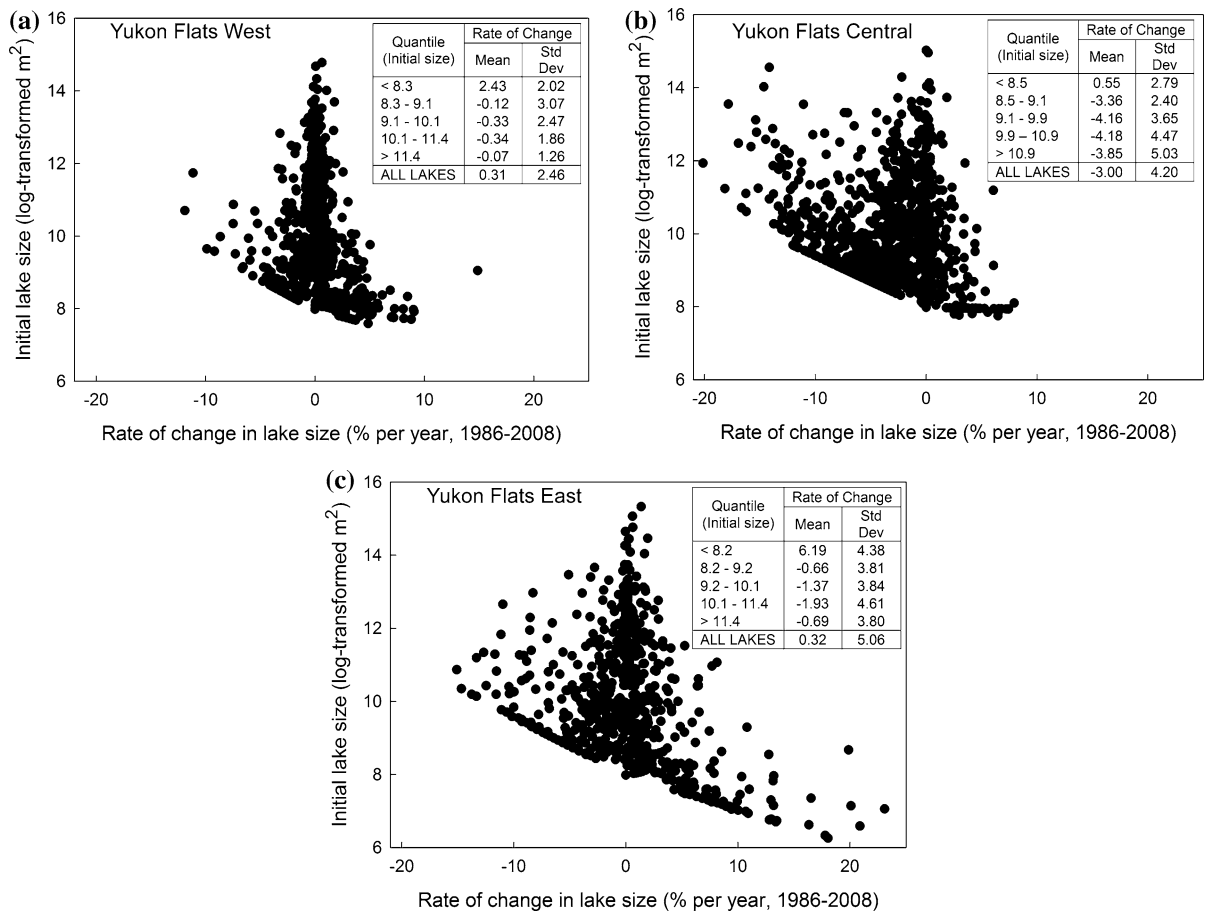
## Future waterfowl species richness projections

We also used lake size projections based on the previously estimated trends from 1986 to 2008 (Roach et al. 2013) to generate plausible future scenarios (in 2025 and 2050) of waterfowl species richness as a result of changing lake size. Similar to the methodology used to generate retrospective projections of waterfowl species richness, we used Monte Carlo simulation (R Core Team 2013) to account for observer variability and the error from both the lake trend and waterfowl species richness models. In addition, we included an initial simulation phase to account for uncertainty in future rates of change that are dependent on the size of a lake at the beginning of a time period of interest.

Plots of lake size in 1986 against annual rates of change in lake size from 1986 to 2008 (Roach et al. 2013) (Fig. 2) indicated that the probability of a particular rate of change depended on a lake's initial size. The smallest lakes tended to have a greater likelihood of increasing, whereas slightly larger lakes had a greater likelihood of decline and very large lakes tended to be more stable. This general 'tilted hat' pattern was present in all three sub-regions (Fig. 2). Thus, instead of assuming a constant rate of change when generating future lake size projections, we adjusted each lake's rate of change for each time period (2010–2025 and 2025–2050) based on its size at the start of that time period. To do this, we defined five quantiles for each sub-region based on initial lake sizes in 1986. Each quantile was characterized by a range of lake sizes and a list of possible rates of change for each range of lake sizes (Fig. 2).

We began each Monte Carlo simulation by taking 100 random draws with replacement from the list of possible rates of change for the quantile that corresponded to the size of each lake at the start of each time period. Lake size at the start of each time period was the mean of the ending lake size distributions that resulted from the previous period's Monte Carlo simulations. Each of these randomly drawn rates of change (i.e., slopes) was then used in conjunction with the size of each lake at the start of the time period as an intercept value to obtain an estimate of lake size at the end of the time period of interest.





**Fig. 2** Relationships between log-transformed lake size in 1986 and rate of change in lake size from 1986 to 2008 for sub-regions in Yukon Flats National Wildlife Refuge, Alaska, USA

(Roach et al. 2013). *Table insets* show the lake size quantiles used for Monte Carlo simulations and summary statistics for each quantile

This initial simulation was then followed by the same two Monte Carlo simulation phases that were used to generate retrospective projections. With the additional simulation phase, this Monte Carlo procedure yielded a distribution of 1,000,000 simulated waterfowl species richness values for each lake which were summarized as before using the median value to represent the species richness projection at each lake and the quartile coefficient of dispersion (Bonett 2006) to represent the error associated with each projection.

#### Study area-wide contemporary species richness projections

We used the waterfowl species richness model to generate contemporary projections of species richness for lakes outside of the three sub-regions but within the

boundaries of our study area ( $n = 2911$ ). Similar to the approach used to generate retrospective projections, we used a two-phase Monte Carlo simulation (R Core Team 2013). The waterfowl species richness model covariates were estimated using the same methods used to generate retrospective and future projections (Appendix 2). However, in contrast to previous temporal projections, we did not have lake trend estimates for these lakes from which to derive the lake size covariate. Thus, to generate contemporary species richness projections for these lakes we estimated the lake size covariate using a lake mosaic that we compiled from various sources (Appendix 2) and held this covariate constant in the first simulation phase. Thus, the only covariate that varied during the first simulation phase was observer. This variable was randomly drawn with replacement from the list of 10

observers for each of the 100 simulations for each lake. The second simulation phase was identical to that used for retrospective projections. These species richness projections were then combined with the retrospective 2010 projections for the three sub-regions to generate a complete map of contemporary species richness projections for the entire study area.

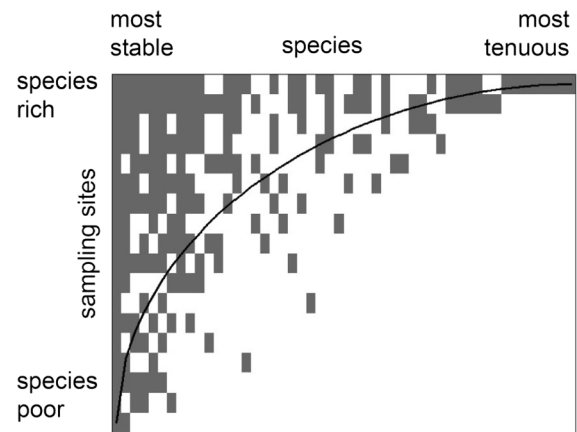
### Habitat heterogeneity versus passive sampling

To evaluate the relative roles of habitat heterogeneity and passive sampling in the ecological processes underlying the waterfowl species richness–lake size relationship, we compared the strengths of the relationships between species richness and lake size and between species richness and the index of habitat diversity that was previously considered as a covariate in the waterfowl species richness model. If habitat heterogeneity was a more important mechanism than passive sampling, we expected that correlations between species richness and the habitat diversity index would be greater than correlations between species richness and natural log-transformed lake size. We assessed these correlations using tests of Pearson's *r*. All assumptions of this test (Kutner et al. 2004) were adequately met.

### Nestedness

To test for the presence of a nested subset structure for waterfowl species at our sample of lakes, we used the BINMATNEST program (Rodríguez-Gironés and Santamaría 2006) (Appendix 3). The BINMATNEST program permutes the columns and rows of a presence–absence matrix (e.g., Fig. 3) until it identifies the maximally nested matrix. In the maximally nested matrix, lakes (i.e., rows) are rank-ordered from top to bottom based on their habitat suitability (i.e., ability to support large numbers of species) and species (i.e., columns) are rank-ordered from left to right based on increasing vulnerability to decreasing lake size (Atmar and Patterson 1993) (Fig. 3).

To evaluate the role of lake size in determining the structure of the maximally nested matrix, we used Spearman's rank correlation to test whether the rank-ordering of lakes in the maximally nested matrix (i.e., a lake's relative ability to support large numbers of species; Fig. 3) was correlated to the rank-ordering of lakes sorted by descending lake size (Lomolino 1996;



**Fig. 3** Example of a maximally nested presence–absence matrix (Simberloff and Martin 1991; R Core Team 2013, vegan package). Gray boxes indicate the presence of a species at a sampling site. The curved black line indicates the boundary of a perfectly packed matrix with the same number of observed species as the data but with no unexpected absences, assuming perfect nestedness. Gray boxes to the right of this line are unexpected presences. White boxes to the left of the line are unexpected absences

Rodríguez-Gironés and Santamaría 2006). All statistical assumptions of the test (Lomolino 1996) were adequately met. To evaluate whether a particular foraging guild (i.e., dabbling vs. diving) was more vulnerable to changing lake size, we used a one-sample runs test for randomness (Daniel 1978) of species guild in the list of species rank-ordered on relative vulnerability to decreasing lake size (i.e., columns of the maximally nested matrix from left to right); assumptions of the test (Daniel 1978) were met.

### Species loss/gain pattern

We estimated the change in waterfowl species richness for each of the 123 sampled lakes between the 2010–2011 field surveys and the 2050 projections. These projected changes, in conjunction with the maximally nested presence–absence matrix derived from our dataset (e.g., Fig. 3), were used to identify the species most likely to be lost or gained at each sampled lake by 2050. Species most likely to be lost at each lake with a projected decline in species richness were the rightmost species of the maximally nested matrix (i.e., most tenuous) that were present at the lake at the time of field surveys (e.g., Fig. 3). Species most likely to be gained at each lake with a projected increase in species richness were the left-most species

(i.e., the most stable) that were absent at the lake at the time of field surveys (e.g., Fig. 3).

Waterfowl species richness projections for the 123 sampled lakes in 2050 were generated using the same Monte Carlo simulation methods (R Core Team 2013) that we used previously to generate future waterfowl species richness projections. However, we used the size of the manually digitized polygons from the Landsat imagery closest to the date of survey to estimate the size of sampled lakes at the start of the 2010–2025 period. These lake size estimates were then used to assign lakes to one of the five quantiles that defined the list of potential rates of change for the 2010–2025 period (Fig. 2). One hundred values were randomly drawn from this list during the initial Monte Carlo simulation phase. When a sampled lake fell outside of the three sub-regions, it was assigned to the nearest sub-region to identify the quantile to be used. As before, we conducted Monte Carlo simulations for the 2010–2025 and 2025–2050 periods, but summarized the species loss pattern for the entire period from 2010 to 2050 for simplicity.

## Results

### Landscape-scale predictors of waterfowl species richness

We observed 31 species of waterfowl (89 % of species on the Refuge list; [http://www.fws.gov/uploadedFiles/bird\\_species\\_list.pdf](http://www.fws.gov/uploadedFiles/bird_species_list.pdf)) (Table 1). Greater (*Aythya marila*) and lesser (*Aythya affinis*) scaups were analyzed as a single species due to the similarity in their ecological niches and the difficulty in differentiating them in the field. The 31 species included 11 with shallow-water affinities (e.g., dabblers, geese, and swans) and 20 with deep-water affinities (e.g., divers and fish-eaters). The mean relative waterfowl species richness at sampled lakes was 8.2 (standard deviation = 3.96,  $n = 123$ ) and ranged from 0 to 18. While species composition varied slightly between sessions and years, the number of species detected in early summer (28), late summer (27), 2010 (27), and 2011 (28) did not vary substantially.

At lakes that were sampled for more than 2 days ( $n = 76$ ), 91 % (standard deviation = 11.4) of species seen within 3 days were detected within 2 days. The additional species that were detected during the third

day did not add to the 31 species detected overall. Thus, our estimates of relative species richness were likely not substantially biased using data from 2 days of sampling.

Relative waterfowl species richness was greatest at lakes that were larger, closer to rivers, had a larger proportion of wetland land cover along their perimeters, and had a larger lake within 5 km ( $\alpha = 0.05$ ; Fig. 4; Table 2). Based on conditional  $R^2$  values (Nakagawa and Schielzeth 2013), these variables accounted for 57 % of the variance in waterfowl species richness with lake size accounting for 54 % of the variance. There were no significant ( $\alpha = 0.05$ ) relationships between these covariates and species richness detectability indices and all  $R^2$  values were  $<0.10$ , indicating that any differences in detectability among lakes did not significantly bias the relationships estimated by the waterfowl species richness model. Of the variables that we did not consider in our model due to their inability to be broadly mapped, only conductivity was significant ( $\alpha = 0.05$ ), and it had very low predictive power ( $R^2 = 0.062$ ), suggesting that we lost relatively little predictive power by not including it.

### Projections of waterfowl species richness

Contemporary study area-wide projections of the number of waterfowl species at individual lakes (i.e., the median of Monte Carlo projections) ranged from 1 to 22 (mean = 5.3, SE = 0.03; Fig. 5). Species richness was spatially heterogeneous throughout the study area and formed distinct hot spots in some areas (Fig. 5).

Across all sub-regions, average species richness per lake was projected to decrease by 11 % from 5.2 species per lake in 1986 to 4.6 species per lake in 2050 (mean change =  $-0.58$ , SE = 0.02; Fig. 6), but rates of change were notably heterogeneous among lakes and within and among sub-regions. From 1986 to 2050, we projected a large decline in average species richness per lake in Yukon Flats Central ( $-1.22$  species, SE = 0.03) from 4.6 species in 1986 to 3.4 species in 2050 ( $-26$  %); a small decline in Yukon Flats East ( $-0.21$  species, SE = 0.04) from 5.7 species in 1986 to 5.5 species in 2050 ( $-4$  %); and a small increase in Yukon Flats West ( $+0.06$  species, SE = 0.02) from 5.6 species in 1986 to 5.7 species in 2050 ( $+2$  %; Figs. 6, 7; Appendices 4–7). Although the East and West sub-regional average changes were

**Table 1** Species expected to be gained or lost by 2050 at 123 sampled lakes in Yukon Flats National Wildlife Refuge, Alaska, USA, based on the maximally nested presence–absence matrix

Common names	Species	Foraging guild	# Lakes inhabited in 2010/2011	# Lakes losing species by 2050	# Lakes gaining species by 2050	Net change in # lakes inhabited by 2050
Pacific loon	<i>Gavia pacifica</i>	Diver	85	0	15	+15
American wigeon	<i>Anas americana</i>	Dabbler	93	0	18	+18
Scaup species	<i>Aythya marila</i> , <i>Aythya affinis</i>	Diver	95	0	12	+12
Mallard	<i>Anas platyrhynchos</i>	Dabbler	87	0	12	+12
Green-winged teal	<i>Anas crecca</i>	Dabbler	58	3	10	+7
Red-necked grebe	<i>Podiceps auritis</i>	Diver	71	7	4	−3
Bufflehead	<i>Bucephala albeola</i>	Diver	62	8	1	−7
Northern shoveler	<i>Anas clypeata</i>	Dabbler	54	13	3	−10
Horned grebe	<i>Podiceps auritis</i>	Diver	60	15	2	−13
White-winged scoter	<i>Melanitta fusca</i>	Diver	57	16	3	−13
Common loon	<i>Gavia immer</i>	Diver	46	17	6	−11
Trumpeter swan	<i>Cygnus buccinator</i>	Dabbler	50	21	1	−20
Northern pintail	<i>Anas acuta</i>	Dabbler	45	25	1	−24
Ring-necked duck	<i>Aythya collaris</i>	Diver	38	19	2	−17
Canvasback	<i>Aythya valisineria</i>	Diver	24	12	0	−12
Common goldeneye	<i>Bucephala clangula</i>	Diver	19	13	1	−12
Canada goose	<i>Branta canadensis</i>	Dabbler	14	8	1	−7
Surf scoter	<i>Melanitta perspicillata</i>	Diver	12	11	1	−10
Greater white-fronted goose	<i>Anser albifrons</i>	Dabbler	9	8	0	−8
Red-throated loon	<i>Gavia stellata</i>	Diver	6	6	0	−6
Barrow's goldeneye	<i>Bucephala islandica</i>	Diver	5	3	0	−3
Red-breasted merganser	<i>Mergus serrator</i>	Diver	5	4	0	−4
Blue-winged teal	<i>Anas discors</i>	Dabbler	3	2	0	−2
Ruddy duck	<i>Oxyura jamaicensis</i>	Diver	4	2	0	−2
Tundra swan	<i>Cygnus columbianus</i>	Dabbler	2	1	0	−1

**Table 1** continued

Common names	Species	Foraging guild	# Lakes inhabited in 2010/2011	# Lakes losing species by 2050	# Lakes gaining species by 2050	Net change in # lakes inhabited by 2050
Common merganser	<i>Mergus merganser</i>	Diver	3	3	0	−3
Redhead	<i>Aythya americana</i>	Diver	1	1	0	−1
Gadwall	<i>Anas strepera</i>	Dabbler	1	1	0	−1
Black scoter	<i>Melanitta americana</i>	Diver	1	1	0	−1
Long-tailed duck	<i>Clangula hyemalis</i>	Diver	1	1	0	−1
American coot	<i>Fulica americana</i>	Diver	1	1	0	−1

Species are listed in the order that they appear (left–right, stable–tenuous) in the maximally nested matrix

relatively small, if they persisted beyond 2050, the compounded rate of change could become substantial. Changes at individual lakes were much more dramatic than sub-region averages, ranging from −9.0 to +6.4 species (−70 to +214 %) from 1986 to 2050 (Fig. 7).

#### Mechanism for the species–area relationship

Habitat diversity did not enter into the waterfowl species richness model as a predictor. Further, the correlation between species richness and the habitat diversity index ( $r = 0.24$ ,  $P = 0.008$ ) tended to be lower than the correlation between species richness and lake size ( $r = 0.50$ ,  $P < 0.0001$ ), suggesting that passive sampling had a greater role than habitat heterogeneity in the ecological mechanism underlying the waterfowl species richness–lake size relationship. Consistent with this, lake size had the greatest effect on species richness among all four of the variables that entered into our waterfowl species richness model (coefficient was  $\sim 3\times$  that of the other variables; Table 2). The proportion of lake perimeter in any wetland land cover type also entered into our final model (Table 2), which suggests that the relative amount of wetland habitat surrounding lakes may be more important to species richness than is shoreline habitat diversity.

#### Predictions of species to be lost or gained at individual lakes

The nestedness temperature of the maximally nested presence–absence matrix (11.6; Fig. 8) was

significantly lower than the temperature of a random matrix ( $P < 0.0001$ ), indicating a non-random pattern of species loss and gain at lakes. The rank-ordering of lakes in the maximally nested matrix was positively correlated with the rank-ordering of lakes sorted by descending size ( $r_s = 0.69$ ;  $P < 0.0001$ ), indicating a role of lake size in determining the pattern of species loss and gain.

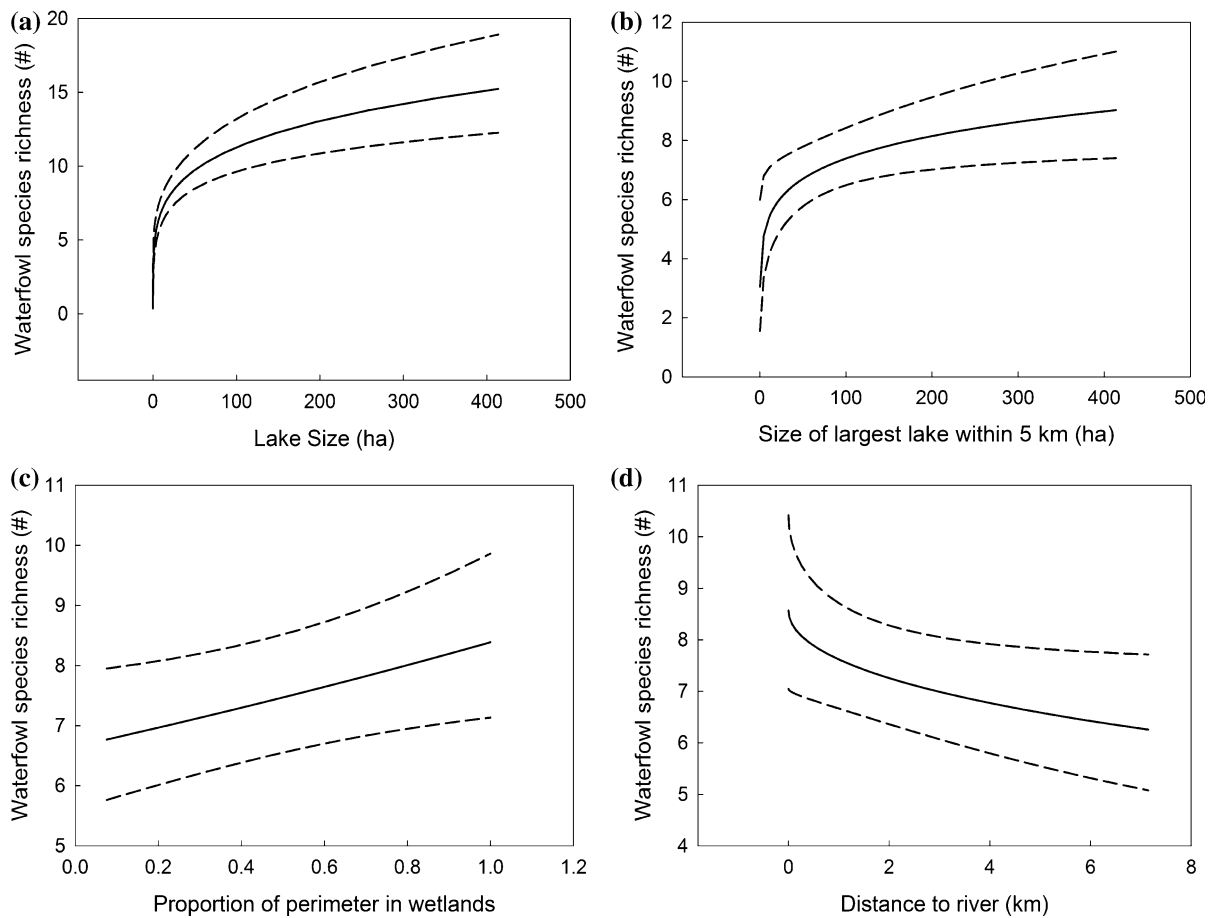
Of the 31 waterfowl species observed at sampled lakes, 25 species were predicted to have a net decline in the number of lakes inhabited by 2050, whereas 6 species were predicted to have a net increase (Table 1). Seven species were predicted to be lost from all (1–6) of the lakes that they inhabited during 2010/2011 (Table 1). The northern pintail (*A. acuta*) was predicted to be lost from the greatest number (24) of lakes (Table 1). There was no significant relationship between species foraging guild (i.e., dabbler vs. diver) and likelihood of species loss ( $P > 0.05$ ).

## Discussion

### Landscape-scale predictors of waterfowl species richness

The large effect of lake size on the number of waterfowl species (Table 2) may be particularly important for land managers in Alaska because substantial declines in lake size have been observed on Alaskan breeding grounds and are expected to continue (Roach et al. 2013). The three variables that were subsidiary to lake size in predicting species





**Fig. 4** Relationships between waterfowl species richness and **a** lake size, **b** size of the largest lake within 5 km, **c** proportion of lake perimeter in a wetland land cover type, and **d** distance to

nearest river based on the waterfowl species richness model, Yukon Flats National Wildlife Refuge, Alaska, USA, 2010–2011. *Dashed lines* indicate 95 % confidence limits

**Table 2** Parameter estimates (centered, scaled, and transformed), standard errors, and *P*-values for tests of the null hypothesis that parameters in the waterfowl species richness

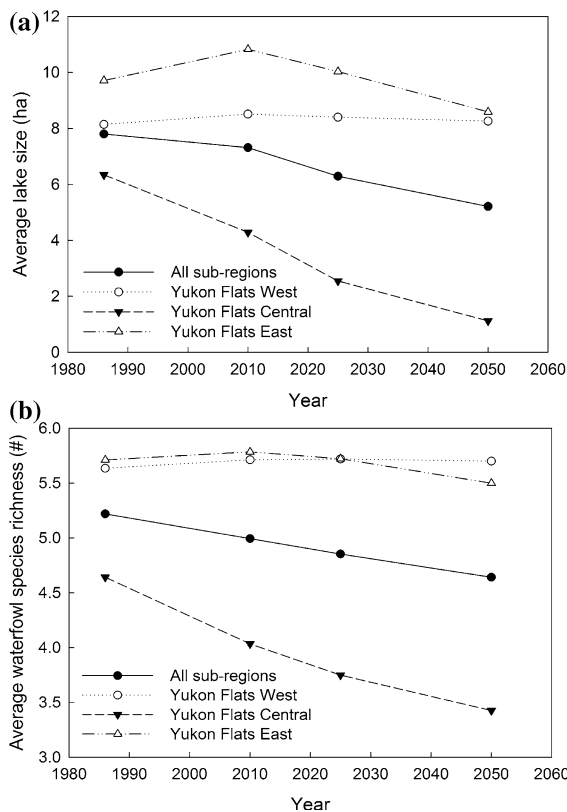
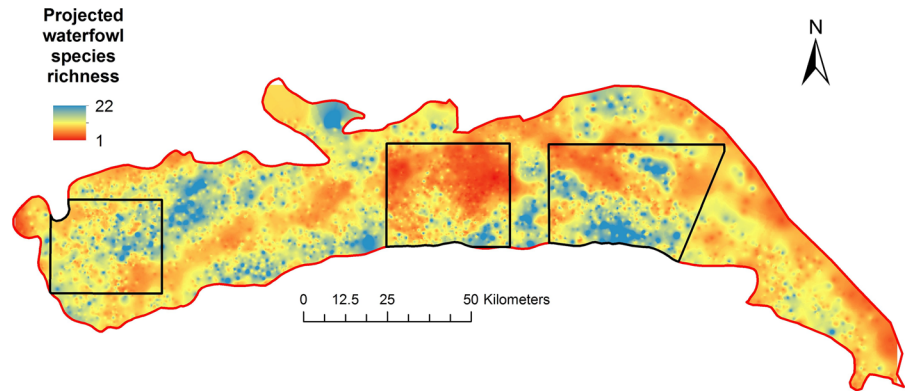
model are equal to zero, Yukon Flats National Wildlife Refuge, Alaska, USA, 2010–2011

Fixed effect	Estimates	Standard error	<i>P</i> value
Intercept	2.03	0.040	<0.0001
Lake size	0.30	0.036	<0.0001
Maximum lake size within 5 km	0.11	0.037	0.014
Proportion of perimeter in wetlands	0.09	0.034	0.030
Distance to river	−0.07	0.032	0.047

richness identified landscape characteristics that may also be important in a management context (Table 2). The influence of the size of the largest lake within 5 km on waterfowl species richness highlights the need to consider the surrounding freshwater matrix when identifying species-rich lakes, particularly when

highly mobile organisms are involved (Haig et al. 1998; Naugle et al. 2001). Consistent with work conducted in more temperate ecosystems (Fairbairn and Dinsmore 2001; Paracuellos and Tellería 2004), we found that wetland vegetation, which can provide high-quality nesting habitat (Krapu et al. 1979; Arnold

**Fig. 5** Study area-wide contemporary projections of individual lake waterfowl species richness, Yukon Flats National Wildlife Refuge, Alaska, USA, 2010–2011. Projections were the median of Monte Carlo projections. *Black lines* indicate boundaries of West, Central, and East sub-regions



**Fig. 6** Retrospective and future projections of **a** average lake size and **b** average species richness for the West, Central, and East sub-regions and all sub-regions combined, Yukon Flats National Wildlife Refuge, Alaska, USA

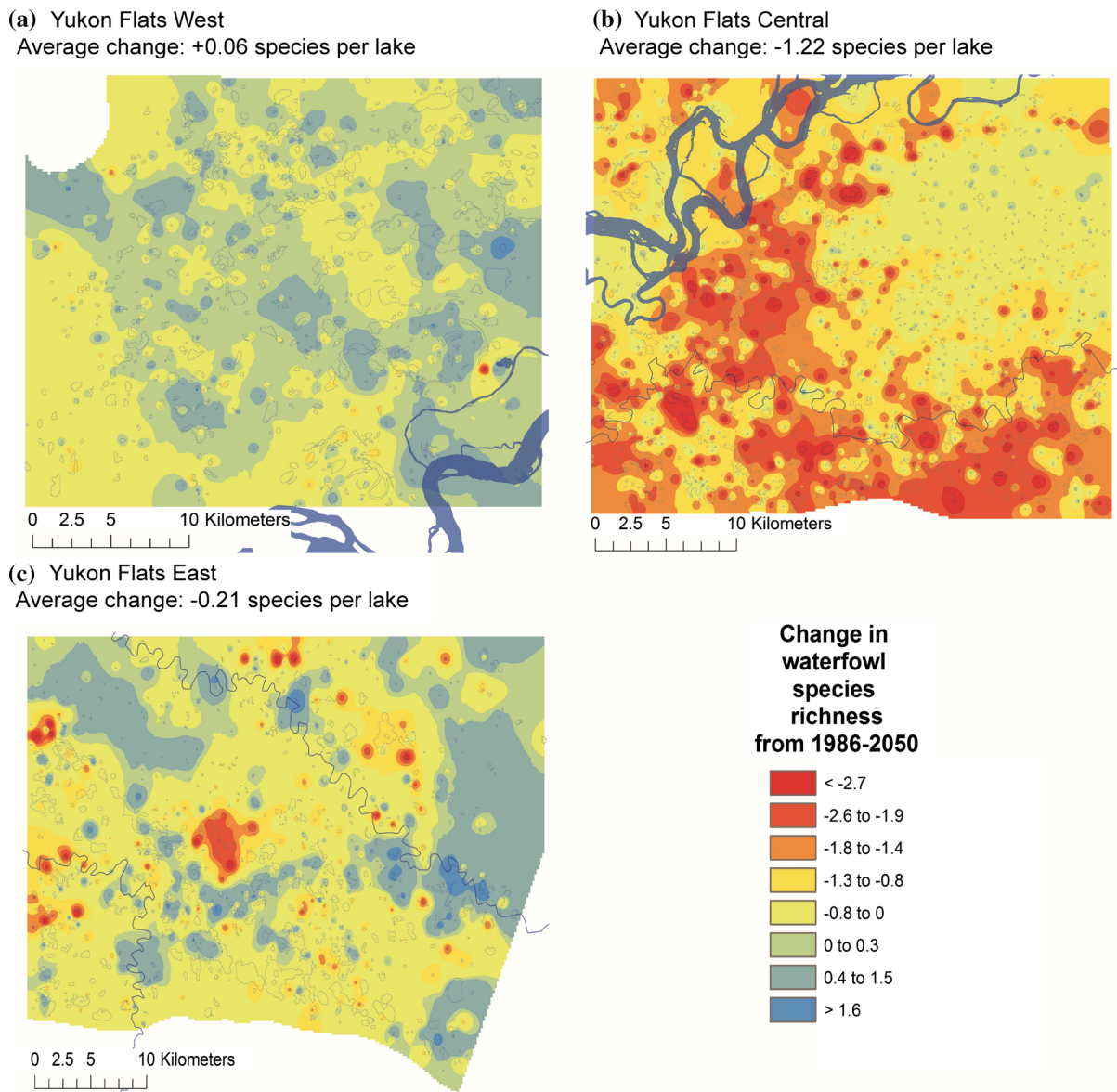
et al. 1993) and protection from predators (Burger 1985), may increase waterfowl species richness (Table 2). An inverse relationship between waterfowl species richness and distance to rivers (Table 2) may reflect a preference of waterfowl for non-shrinking

lakes that may be either periodically recharged by fluvial flood events or have their water levels maintained by beaver activity (Hood and Bayley 2008).

#### Projections of waterfowl species richness

Using quantitative relationships between landscape characteristics, lake size trends, and waterfowl species richness, we developed maps that identify individual lakes and sub-regions where losses in species richness have been and are expected to be the greatest (Fig. 7). As a result of declines in lake size, we projected a relatively large net loss in species richness from 1986 to 2050 across all three sub-regions (−11 %) and even larger losses for individual lakes (up to −70 %) and sub-regions (−26 % in Yukon Flats Central; Fig. 7). Rates of change were heterogeneous both within and among sub-regions.

Two factors likely contributed to this among-region heterogeneity in species richness projections. First, Yukon Flats Central had lakes that were located farther from rivers (mean = 2.75 km, SE = 0.08) than the East (mean = 1.64 km, SE = 0.06) and West sub-regions (mean = 1.43 km, SE = 0.04), and tended to have low initial species richness (Fig. 4d) and lakes likely to shrink as a result of climate warming (Roach et al. 2013). Lakes far from rivers may be more likely to shrink due to infrequent recharge events (Roach et al. 2013) and the declining water levels at these lakes may support fewer species compared to lakes closer to rivers. Second, the Central sub-region had the smallest lakes (Fig. 6a) that fell along a steeper section of the species–area curve (Fig. 4a) where species richness was low and changes in species richness were proportionally large for a unit change in

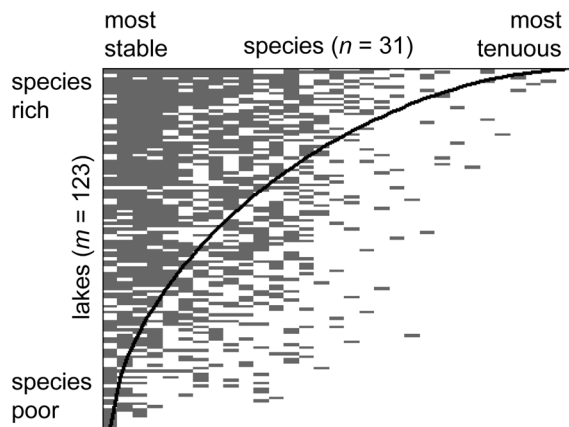


**Fig. 7** Projected changes in waterfowl species richness from 1986 to 2050 at lakes in the West, Central, and East sub-regions, Yukon Flats National Wildlife Refuge, Alaska, USA

area. This result is in contrast to the flatter section of the curve at larger lake sizes, such as those found in the East and West sub-regions. This asymptotic-like nature of the species–area curve (Fig. 4a) emphasizes the role that region-specific lake size can have in determining the magnitude of the effect of declining lake size on species richness.

Land managers may be able to use our multi-scale species richness projections to attain conservation goals. The Refuge is characterized by substantial

inholdings of native allotments affected by the Alaska National Interest Lands Conservation Act. As a result, land exchanges involving inholdings and Refuge lands are one potential tool for approaching conservation goals. At the sub-regional scale, Yukon Flats East and West (Fig. 6b) had the greatest initial species richness and were projected to remain stable in species richness through 2050. Since these sub-regions are at little risk from loss of species richness, conservation may be the best strategy. In contrast, the Central sub-region had



**Fig. 8** Maximally nested presence-absence matrix for 123 lakes in Yukon Flats National Wildlife Refuge, Alaska, USA, 2010–2011. *Gray boxes* indicate the presence of a species at a lake. The *curved black line* indicates the boundary of a perfectly packed matrix with the same number of observed species as our data but with no unexpected absences, assuming perfect nestedness. *Gray boxes* to the *right* of this *line* are unexpected presences. *White boxes* to the *left* of the *line* are unexpected absences

both low initial species richness and the largest projected declines, so lands within this sub-region may be candidates for exchange for more desirable inholdings within the Refuge boundary. At a smaller scale (within sub-regions), by identifying areas with landscape metrics that support a large number of species (e.g., large lakes, close to rivers; Fig. 4), managers may be able to locate smaller areas suitable for exchange or focused monitoring. This multi-scale land exchange strategy may also be broadly applicable to other Alaskan NWRs that exhibit a similar degree of heterogeneity in lake change (Roach et al. 2013), landscape metrics, and within-Refuge-boundary ownership.

The “tilted hat” pattern that characterized the dependence of rates of change on initial lake size (Fig. 2) highlights nonlinear lake properties that may promote some degree of resilience to climate warming. First, there may be an underlying cyclical pattern of lake growth and decline. The bottom portion of the “tilted hat” pattern (i.e., for relatively small lakes) shows the smallest lakes have the greatest likelihood of increasing and as lakes get larger they are more likely to shrink (Fig. 2). Second, the top portion of the hat indicated that the largest lakes that support the most species have a high likelihood of remaining

stable. However, it is important to note that despite this cyclical nature of lake size change, the mean of each distribution remained centered on a long-term rate of change that was different from zero (Fig. 2). Thus, by taking random draws from these distributions, our future projections of species richness were informed by each sub-region’s unique long-term rate of change estimated from 1986 to 2008 along with each sub-region’s underlying cyclical dynamics. In the future, a better understanding of the effects of climatic drivers on lake change may allow the use of climate models to further improve these projections of species richness.

### Ecological mechanisms for the species–area relationship

Our sampling design made sampling artifact an unlikely explanation for our observed species–area curve. Because sampling ceased either at 6 h after sunrise or when an entire lake perimeter had been sampled, small lakes often had their entire perimeters sampled, and thus were more intensively sampled per unit area compared to larger lakes. The effect of incomplete sampling for large lakes would be to depress the species–area curve at large lake sizes (Fig. 4a), an effect opposite of that expected from sampling artifact. This bias would not affect the rank-ordering of species richness projections among different lakes and different time periods.

Our findings supported a predominant role of passive sampling, rather than habitat heterogeneity, as the ecologically based mechanism of the SAR. Large lakes appeared to have more species primarily because they provided more space and resources (Patterson 1976; Nudds and Ankney 1982), rather than a greater diversity of shoreline habitats surrounding lakes. Because passive sampling and habitat heterogeneity are not necessarily mutually exclusive (Connor and McCoy 2001), and because we did detect relatively weak effects of habitat heterogeneity on species richness, future work should continue to evaluate the habitat heterogeneity hypothesis in comparison to competing hypotheses. Future investigations could also evaluate relationships between species richness and fine-scale variables that we were not able to project across the landscape such as lake depth, lake productivity, aquatic vegetation, and invertebrate food resources.

## Identification of vulnerable species

An understanding of the ecological mechanisms underlying SARs may help land managers to identify the species most vulnerable to habitat loss. Because passive sampling had a greater role than habitat heterogeneity in the mechanism underlying the waterfowl–lake size relationship, it is unlikely that one species guild (i.e., group of species with a particular habitat preference) would be more affected by changing lake size than another. This idea is consistent with the patterns observed in the maximally nested presence–absence matrix (Fig. 8; Table 1), where the relative vulnerability of species was not related to foraging guild (i.e., dabbler vs. diver). Instead, the 16 rightmost (i.e., most tenuous) species in the maximally nested presence–absence matrix consisted of species listed as uncommon, occasional, or rare on the Refuge species list ([http://www.fws.gov/uploadedFiles/bird\\_species\\_list.pdf](http://www.fws.gov/uploadedFiles/bird_species_list.pdf)). Thus, the vulnerability of waterfowl species to decreasing lake size may be related more to a species' rarity due to its being at the edge of its range rather than to its foraging guild or preference for a particular habitat.

Our rank-ordering of individual waterfowl species in terms of their relative vulnerability to decreasing lake size (Table 1) provides a means for refuges to target species for closer monitoring or additional conservation efforts. For example, seven rare species are expected to be absent from our suite of sampled lakes by 2050 [Table 1; red-throated loon (*Gavia stellata*), common merganser (*Mergus merganser*), redhead (*Aythya americana*), gadwall (*A. strepera*), black scoter (*Melanitta americana*), long-tailed duck (*Clangula hyemalis*), and American coot (*F. americana*)], whereas northern pintails (*A. acuta*) are expected to be absent from 25 of our sample lakes by 2050. In contrast, by 2050, five species are expected to occupy 12–19 % more lakes than they did in 2010–2011 [Table 1; Pacific loon (*Gavia pacifica*), American wigeon (*Anas americana*), scaup (*A. marila*, *A. affinis*), mallard (*A. platyrhynchos*), and green-winged teal (*Anas crecca*)]. It is important to reiterate that these are lake-specific estimates and even though the richness may change at individual lakes, we do not expect broader-scale extinction such as from all boreal forest wetlands or the Refuge as a result of lake change within our projection limits.

Populations situated near the periphery of a species geographic distribution tend to exhibit lower abundance and greater temporal variability in abundance (Channell and Lomolino 2000). This reduced abundance and greater variability are generally thought to be driven by reduced habitat quality along the periphery (Curnett et al. 1996; Vucetich and Waite 2003). Therefore, peripheral populations of a species may be most vulnerable to shrinking lake size because they are located in an already low-quality habitat where other, potentially compensating, habitat features may not be present.

## Methodological framework for quantifying effects of landscape change

This work provides a novel space-for-time analytical framework that can be used to quantify the effects of landscape change on a range of metrics relevant to scientists, land managers, and policy makers. Because our approach generated spatially explicit projections for individual lakes, our sampling sites can be revisited in the future and the robustness of our predictions can be assessed. The presence of a SAR for waterfowl species at lakes in the Refuge provided the necessary framework for generating species richness projections and for understanding the effects of shrinking lakes on waterfowl in Alaska. Others can use our general approach of quantitatively linking empirically based relationships between landscape features (e.g., lake size) and a response variable of interest (e.g., species richness) to estimate long-term changes in those landscape features. These efforts may enable managers to move beyond describing landscape change toward quantifying the effects of landscape change on the management target (i.e., ecosystem services) they are tasked to protect.

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